DOI: 10.1111/j.1570-7458.2009.00838.x

Ultraviolet and violet light: attractive orientation cues for the Indian meal moth, *Plodia interpunctella*

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Accepted: 26 January 2009

Key words: foraging, Lepidoptera, Pyralidae, phototactic response, biological control, electroretinogram

Abstract

The Indian meal moth (IMM), *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), engages in long-distance or foraging flights in the twilight hours of the scotophase when blue light dominates the irradiance spectrum of the sky. We tested the hypothesis that IMM uses wavelengths of visible blue/violet light as orientation cues that trigger phototactic responses. In four-choice laboratory experiments, blue light (400–475 nm) was significantly more effective than green (475–600 nm), orange (575–700 nm), or red (590–800 nm) light in attracting males and mated females. In subsequent experiments that tested light emitting diodes (LEDs) emitting peak wavelengths in the blue/violet-light range, the 405-nm 'violet' LED was significantly more effective than the 435-, 450-, or 470-nm 'blue' LED in attracting males as well as virgin and mated females. In electroretinogram recordings, the 405-nm wavelength elicited significantly stronger receptor potentials from female and male eyes than the 350-nm (UV) wavelength, and in a behavioral experiment it significantly enhanced the known attractiveness of UV light. Equal attraction of IMMs to 405-nm LEDs at 600–700 $\mu W/cm^2$ with or without UV light, and significantly stronger attraction to a 405-nm LED than to a 350-nm LED at maximum light intensities, suggest that the deployment of violet instead of UV light could become one of several management tactics for control of IMMs.

Introduction

The use of light as navigational or directional orientation cue has been well-studied in diurnal insects (Wehner, 1984; Wehner & Muller, 2006; Hironaka et al., 2007; Pfeiffer & Homberg, 2007), but has been investigated for only a few insects active in crepuscular or nocturnal light with inherently diverse irradiance spectra (e.g., Warrant et al., 2004; Theobald et al., 2007). Blue wavelengths become dominant ('blue-shifted') as the solar elevation angle decreases and the sun disappears below the horizon. Under starlight, irradiance spectra are 'red-shifted' and strongly influenced by the presence or absence of the moon (Johnsen et al., 2006). For 1–2 h between sunset and astronomical twilight, blue-shifted twilight offers a constant polarization pattern in non-cloudy skies that provides insects with orientation cues (Cronin et al., 2006). The specialized dorsal rim area of the eye of the desert locust, Schistocerca gregaria (Forskal), with peak sensitivity for polarized blue light, is likely an adaptation for nocturnal flight (Homberg, 2004). Moonlight and artificial light are also known to serve as directional cues. Black carpenter ants, *Camponotus pennsylvanicus* (DeGeer), can use moon light or artificial light to orient themselves along trails (Klotz & Ried, 1993). Similarly, polarized moon light as well as non-polarized natural and artificial light sources serve foraging dung beetles, *Scarabaeus zambesianus* Péringuey, as orientation cues when they return to their harborage (Dacke et al., 2004). Attraction of nocturnal moths to light may be due, in part, to a shift in orientation response from moonlight to artificial light (Baker & Sadovy, 1978).

The Indian meal moth (IMM), *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), is one of the most serious and wide-spread pests of stored products (Zhu et al., 1999; Nansen & Phillips, 2004). It is most active in the first 2 h of the scotophase (twilight conditions). As an enduring flyer, it can travel over a large spatial scale (Campbell & Arbogast, 2004). We argue that during long-distance flights, IMM is dependent upon visual orientation

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or foraging cues that are perceived by photoreceptors adapted to function under blue-shifted twilight.

Previous studies have investigated the response of IMMs to ultraviolet (UVA; 345–400 nm) and green light (480–580 nm). In electoretinogram studies, Marzke et al. (1973) demonstrated that IMM eyes respond to wavelengths ranging from 350 to 650 nm, with the strongest responses to green light. In behavioral studies, Stremer (1959) demonstrated that IMMs are most strongly attracted to UV (365 nm) and green (580 nm) lights, suggesting that the eyes are potentially dichromatic. He further showed that high-intensity light is more effective than low-intensity light in attracting moths. Kirkpatrick et al. (1970) confirmed that IMMs are attracted to UV light alone and in combination with green light, with no significant preference for either stimulus. Using non-standardized stimuli with respect to light energy, Soderstrom (1970) showed that traps fitted with eight green lights captured significantly more IMMs than traps fitted with one UV light. Most recently, Sambaraju & Phillips (2008) reported that IMMs preferred resting in areas illuminated with UV, green or white light to resting in dark areas, and that they exhibited the strongest phototactic response to UV light.

Here we show that (i) blue light (400–475 nm) is more attractive to IMM than green (475–600 nm), orange (575–700 nm), or red (590–800 nm) light; (ii) a 405-nm 'violet' light emitting diode (LED) is more attractive than a 435-, 450-, or 470-nm 'blue' LED; (iii) a 405-nm LED elicits stronger receptor potentials from female and male eyes than a 350-nm UV LED; and (iv) that at maximum light intensities a 405-nm LED is significantly more attractive than a 350-nm LED.

Materials and methods

Origin and maintenance of Indian meal moth colony

Indian meal moth larvae were obtained from infested cereal bars. Larvae were reared at 25–27 °C at a photoperiod of L17:D7. The rearing diet was modified from LeCato (1976), and consisted of whole wheat flour (27.5% by volume), yellow cornmeal (27.5%), Purina One dog food (13.5%), brewers yeast (6.9%), honey (6.9%), glycerine (6.9%; 96% pure), Quaker rolled oats (6.8%), and wheat germ (3.4%).

Fifth-instars were separated by sex and placed in groups of 12–15 specimens into Petri dishes (10 cm diameter) containing corrugated cardboard as pupation sites. Eclosed adults were kept at both reversed and staggered photoperiods to allow experimentation throughout the entire day. To obtain gravid females, 2–3 virgin females and 3–4 virgin males were confined in small cages (10×10 cm) during the scotophase. The next day, females were assumed mated and used for colony rearing or laboratory experiments. All adult moths used in experiments were 2–5 days old.

General experimental design

Still-air four- or two-choice laboratory experiments (Figure 1A,B) were conducted in a modified wind tunnel ($1.1 \times 1.1 \times 3.3$ m long), with air entry and exit sections covered by mesh screens and by black paper to minimize light reflections. For each replicate, two Petri dishes with five insects each were placed on a 50-cm tall, black felt-covered platform (23×30 cm) in the centre of the tunnel. Light sources as test stimuli were randomly assigned to, and mounted within, adhesive-lined green Delta traps (Contech, Delta, British Columbia, Canada), assuming that a strong orientation cue would be attractive to flying moths and that trap catches could serve as a measure of the strength of the orientation response. In four-choice experiments, traps were randomly placed in each corner of the tunnel ca. 80 cm apart from each other and 1.5 m from the release platform (Figure 1A). They were positioned at a 15° angle directed towards the release stand (Figure 1A). Each stimulus was rotated clockwise after every replicate to determine whether IMM orient to a particular light source regardless of its position inside the wind tunnel.

For two-choice experiments, light sources were placed inside adhesive-lined green Delta traps, and positioned at opposite ends of the wind tunnel (Figure 1B). Lights were randomly assigned to each side and then alternated for each replicate. All experiments were conducted in the first 2 h of the 7-h dark phase, when IMMs are searching for mates (males) or suitable oviposition sites (females).

An experimental replicate was initiated by lifting the lid of each Petri dish on the release platform, and was terminated by scoring the number of moths captured in each trap 2 h later. All moths not responding were removed from the wind tunnel prior to initiating a new experimental replicate. After each set of four replicates, the wind tunnel was wiped with 70% ethanol and left to dry overnight.

Electroretinogram recordings

Insects were immobilized laterally with modeling clay (Sargent Art, Hazleton, PA, USA) on an adhesive-coated glass slide. Both antennae and the left wing were removed to ensure access of tungsten electrodes that had been electrically sharpened (Cool et al., 1970). The indifferent electrode was micro-manipulated (Leitz micromanipulator M; Leitz, Vienna, Austria) into the thorax and the recording electrode into the equatorial region of the eye near the left edge, thus preventing light shadows. Electrical

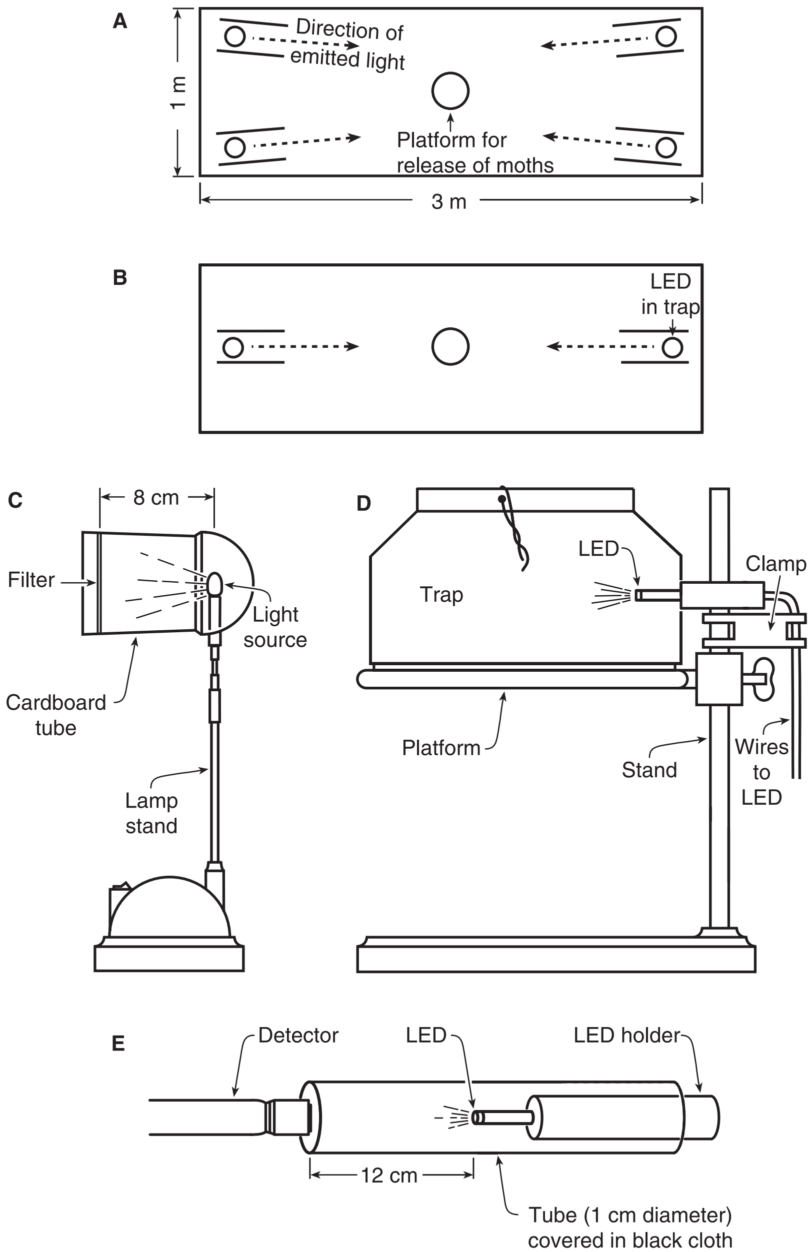

Figure 1 Experimental design to test behavioral responses of *Plodia interpunctella* in (A) four- and (B) two-choice experiments; (C) light source for testing portions (blue, green, orange, red) of visible light; (D) mounting of a light-emitting diode (LED) within a green Delta trap; (E) set-up for measurement of spectral composition and light intensity of light-emitting diodes. All drawings are not to scale.

potentials from the eye in response to test stimuli were pre-amplified (Syntech Auto Spike; Syntech, Hilversum, The Netherlands) and recorded with an electroantennogram (EAG) oscilloscope program (Syntech). Based on the signal-to-noise ratio, potentials of >5 mV were considered responses. Experiments were conducted inside a light-proofed Faraday cage mounted on a steel table to limit vibration. Because results of preceding experiments affected the design of subsequent experiments, specific methods are further reported in the Results.

Statistical analysis

Ten replicates were conducted for each behavioral experiment, but replicates without any responding insects were excluded from statistical analysis. Percent trap captures in all replicates of four-choice experiments with responding insects were arcsine-transformed and subjected to the Kruskal–Wallis test for non-parametric data followed by the Student–Newman–Keuls analog for multi-comparison of means (Zar, 1999). Data obtained in binary-choice experiments and in electroretinogram

recordings were analyzed by the Wilcoxon rank sum test. All data analyses employed JMP software (SAS®, Cary, NC, USA).

Results

Experiments 1–3: attractiveness of blue, green, orange, and red light

To determine the portion of visible light that constitutes the strongest visual orientation cue for IMM, a modified desk lamp (Espressivo, Ikea) with a 20-W halogen bulb was used as a light source (Figure 1C). Males (experiment 1, n = 10), virgin females (experiment 2, n = 10), and mated females (experiment 3, n = 10) were used as bioassay insects. The desk lamp was connected to a rheostat to adjust light intensities, and the halogen bulb was fitted with a black cardboard cylinder (8 × 12 cm wide), with the light filters mounted at the front, 8 cm apart from the bulb (Figure 1C). The cylinder projected the light in one direction.

Flexible filters (Lee Filters, Hamshire, UK) generated light spectra in the range of blue (400–475 nm, peaks at 444 and 594 nm; referred to as 'Rose Purple 7'), green (475–600 nm, peak at 532 nm; 'Lime 8'), orange (525–750 nm, peak merging with infrared; 'Orange 9'), and red (590–750 nm, peak merging with infrared; 'Light Red') (Figure 2A–D). The orange filter, permitting passage of 560–600-nm yellow wavelengths, substituted for a narrow-band yellow filter that was not obtainable. Any attraction to the orange filter was assumed to be due to yellow wavelengths because IMMs have a low relative response to red wavelengths (Stremer, 1959).

Light intensities were measured with an HR4000 high-resolution spectrometer (Ocean Optics, Dunedin, FL, USA) fitted with a cosine corrector at the detector. All light sources were tested at an intensity of 15 $\mu W/cm^2$ (the maximum intensity of light obtainable from the blue filter), integrated from 350–700 nm, and measured at the filter held 8 cm from the halogen bulb.

In experiments 1–3, significantly more males and gravid females were captured in traps emitting blue light than in traps emitting green, red, or orange light (Figure 3, experiments 1 and 3). Virgin females were not very responsive and exhibited no preference for either spectrum of light (Figure 3, experiment 2).

Experiments 4–6: attractiveness of wavelengths in the blue range (400–475 nm)

Experiments 4–6 were designed to determine the wavelengths in the blue range most effective in attracting males (experiment 4, n = 10), virgin females (experiment 5, n = 10), and mated females (experiment 6, n = 10). Light-emitting diodes (Roithner Lasertechnik, Vienna, Austria) with peak wavelengths of 405 nm (range 400–410 nm), 435 nm (410–470 nm), 450 nm (440–460 nm), and 470 nm (465–475 nm) (Figure 2H–K) were tested in four-choice experiments. For each replicate, one of the four LEDs was randomly assigned to, and mounted within, green Delta traps (Figure 1D; see general experimental design), using an LED controller to adjust the intensity of each LED to 200 $\mu W/cm^2$ integrated from 350 to 550 nm. Each LED was calibrated by inserting it into a ridged black cloth-covered plastic tube (28 × 1 cm) 12 cm apart from the light detector positioned at the opposite end of the tube (Figure 1E). Compared to experiments 1–3, light intensities were increased to help maintain or even increase the high percentage of responding insects.

In experiments 4–6, significantly more males (experiment 4), virgin females (experiment 5) and mated females (experiment 6) were captured in traps fitted with the 405-nm LED than in traps fitted with the 435-, 450-, or 470-nm LED (Figure 4).

Experiments 7–9: attractiveness of wavelengths in the ultraviolet/violet range (350–405 nm)

To determine the wavelength(s) in the UV- and violet-light range that are the most effective orientation cues, LEDs with peak wavelengths of 350, 365, 380, and 405 nm (integrated from 300 to 450 nm) were tested with males (experiment 7, n = 10), virgin females (experiment 8, n = 10), and mated females (experiment 9, n = 10). Experimental design and calibration method were identical to those described for experiments 4–6.

In experiment 7, the 350- and 380-nm LEDs were equally effective in attracting males, but the latter was not more effective than the 365- and 405-nm LED (Figure 5). In experiment 8, the 350-, 365-, 380-, and 405-nm LEDs all were equally ineffective in attracting virgin females (Figure 5). In experiment 9, the 350-nm LED attracted significantly more mated females than did the 365-, 380-, and 405-nm LEDs (Figure 5).

Experiments 10–13: attractiveness of ultraviolet and violet light singly or in combination

Given the strong attraction of IMM to the 405- (violet) and 350-nm (UV) LEDs in experiments 4–6 and 7–9, respectively, experiments 10–13 explored whether violet and UV wavelengths are more attractive in combination than on their own. Two different experimental designs were deployed. The first design tested one 405-nm LED (132 $\mu W/cm^2$) and one 350-nm LED (68 $\mu W/cm^2$) with a combined light intensity of 200 $\mu W/cm^2$/trap as the treatment stimulus vs. a control stimulus that consisted of two 350-nm LEDs with a combined light intensity of 200 $\mu W/cm^2$/trap (integrated from 300 to 450 nm) for attraction of males (experiment 10, n = 10), virgin females

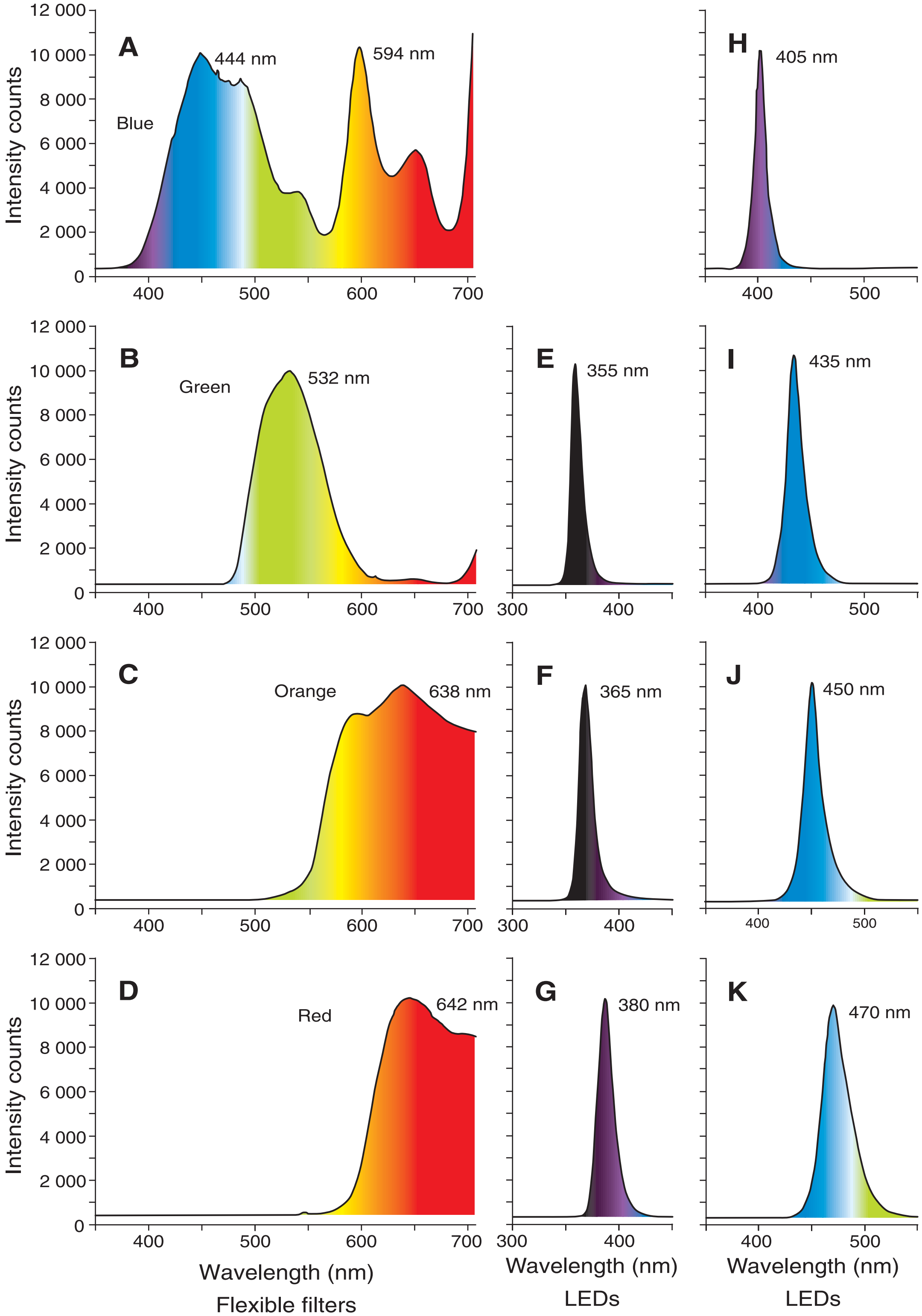

Figure 2 Spectral composition of light stimuli bioassayed in experiments 1–16. Stimuli A–D were generated through flexible filters coupled with a 20-W halogen bulb (see Materials and methods for detail), whereas stimuli E–K were generated through light-emitting diodes. In A–K, the wavelength with the highest intensity is indicated.

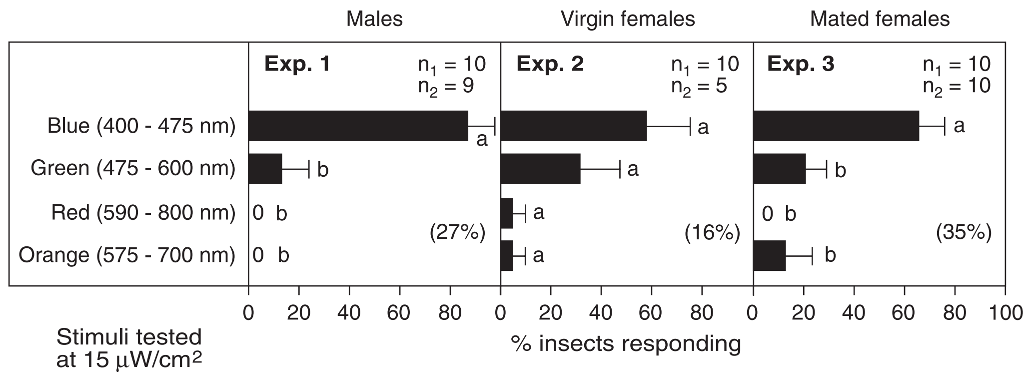

Figure 3 Mean (+ SE) percent of male, virgin female, and mated female *Plodia interpunctella* responding in four-choice experiments 1, 2, and 3, respectively, to spectra of visible light (Figure 2). In each experiment, n_1 is the number of replicates that were tested and n_2 is the number of replicates that yielded responding insects. The overall percentage of responding insects is given in parentheses. Bars with the same letter within an experiment are not significantly different (Kruskal–Wallis test followed by the Student–Newman–Keuls analog: P>0.05).

(experiment 11, n = 10), and mated females (experiment 12, n = 10). The second design tested the same treatment stimulus vs. a control stimulus that consisted of two 405-nm LEDs with a combined light intensity of 200 µW/cm²/trap (integrated from 300 to 450 nm) for attraction of mated females (experiment 13, n = 10). Only mated females were tested for the second design because mated females appeared to respond best in preceding experiments. Emission of the 405-nm wavelength at intensities twice as high as the UV wavelength in combined light sources was based on proportionately higher levels of violet light at sunset and twilight (Robertson, 1966; Johnsen et al., 2006).

In experiments 10–12, the two 350-nm LEDs attracted as many males, virgin females, and mated females as did the 350- and 405-nm LEDs in combination (Figure 6). In experiment 13, the two 405-nm LEDs attracted as many gravid females as the combined 350- and 405-nm LEDs (Figure 6).

Experiment 14: attractiveness of single and dual light sources of identical intensities

In preparation for experiment 15, experiment 14 (n = 10) determined whether stimuli of identical light intensity emitted from one or two light sources are equally effective in attracting IMMs. Thus, one 405-nm LED at 200 µW/cm² (integrated from 350 to 450 nm) was tested vs. two 405-nm LEDs each at 100 µW/cm² (integrated from 350 to 450 nm). Only males were tested because in experiments 4–6 the insects' response to the 405-nm wavelength appeared not affected by their gender or mating status. In experiment 14, one 405-nm LED at 200 µW/cm² and two

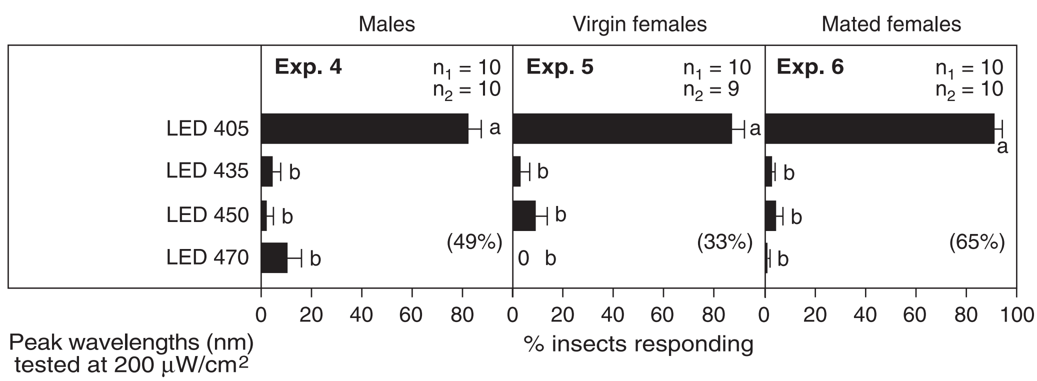

Figure 4 Mean (+ SE) percent of male, virgin female, and mated female *Plodia interpunctella* responding in four-choice experiments 4, 5, and 6, respectively, to light-emitting diodes with peak wavelengths of 405, 435, 450, or 470 nm. Additional information is provided in the legend of Figure 3.

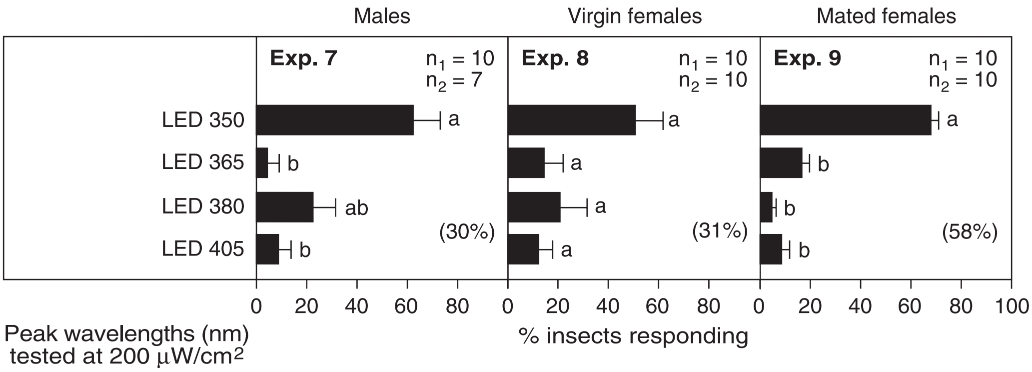

Figure 5 Mean (+ SE) percent of male, virgin female, and mated female *Plodia interpunctella* responding in four-choice experiments 7, 8, and 9, respectively, to light-emitting diodes, emitting ultraviolet or violet light at peak wavelengths of 350, 365, 380, or 405 nm. Additional information is provided in the legend of Figure 3.

405-nm LEDs at 100 µW/cm^2 each were equally effective in attracting males (Figure 7).

Experiments 15–17: effects of light intensity and wavelength combination

Considering that (i) high-intensity light is more effective than low-intensity light in attracting IMMs (Stremer, 1959), and (ii) a 350-nm LED emits on average not more than 100 µW/cm^2, experiment 15 investigated whether attractiveness of a 350-nm LED (100 µW/cm^2) could be enhanced by combining it with a 405-nm LED that emitted a light intensity of 600 µW/cm^2 (integrated from 300 to 450 nm) instead of merely 132 µW/cm^2, as in experiments 10–13. The control stimulus consisted of two 350-nm LEDs with a combined light intensity of 100 µW/cm^2 (integrated from 300 to 450 nm).

The significantly stronger response of mated females in experiment 15 to the 350- and 405-nm LED combination could have been due to its higher light intensity or particular wavelength combination. Thus, experiment 16 (n = 10) tested both stimuli at identical light intensity (700 µW/cm^2) but contrasting light composition. Stimulus 1 consisted of two 405-nm LEDs at 600 and 100 W/cm^2, respectively (integrated from 300 to 450 nm), whereas stimulus 2 consisted of one 405-nm LED at 600 µW/cm^2 and one 350-nm LED at 100 µW/cm^2 (integrated from 300 to 450 nm).

With light intensity affecting the attractiveness of multiple LED light sources in experiments 15 and 16, experiment 17 (n = 10) tested one 405- vs. one 350-nm LED at maximum intensities of ca. 100 and 1800 µW/cm^2, respectively. In experiment 15, the combination of one

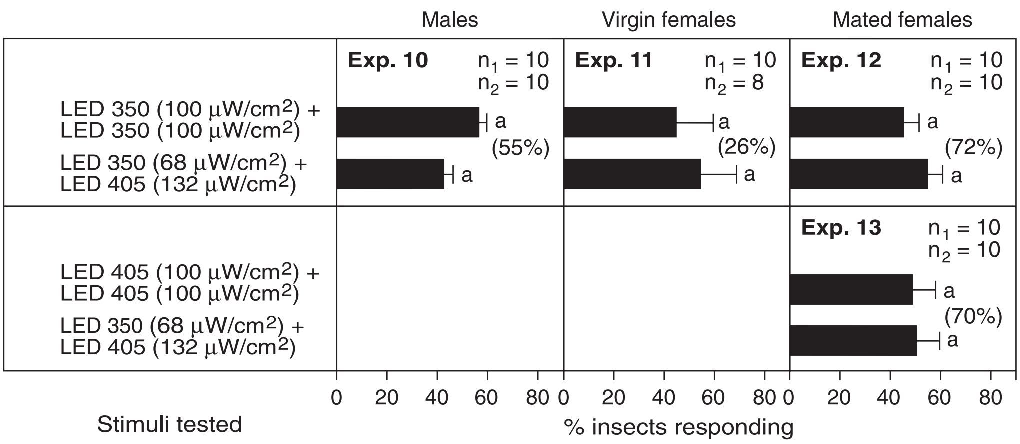

Figure 6 Mean (+ SE) percent of male, virgin female, and mated female *Plodia interpunctella* responding in two-choice experiments 10–13 to combinations of light-emitting diodes, emitting ultraviolet or violet light at peak wavelengths of 350 or 405 nm. Additional information is provided in the legend of Figure 3. In each experiment, bars with the same letter are not significantly different (Wilcoxon rank sum test: P>0.05).

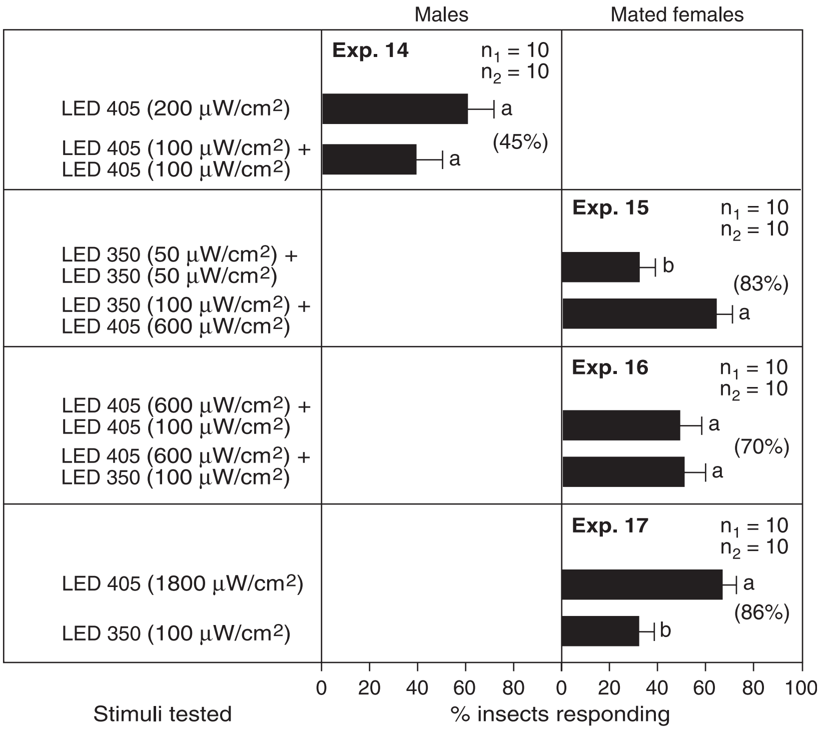

Figure 7 Mean (+ SE) percent of male or mated female *Plodia interpunctella* responding in two-choice experiments 14–17 to light-emitting diodes, emitting violet light or ultraviolet light at peak wavelengths of 405 or 350 nm. Additional information is provided in the legend of Figure 3. In each experiment, bars with the same letter are not significantly different (Wilcoxon rank sum test: P>0.05).

350- and one 405-nm LED at a combined light intensity of 700 μW/cm^2 attracted significantly more mated females than did two 350-nm LEDs at a combined light intensity of 100 μW/cm^2. In experiment 16, with each stimulus at the same combined light intensity of 700 μW/cm^2, the two 405-nm LEDs attracted as many mated females as did one 350- and one 405-nm LED (Figure 7). In experiment 17, one 405-nm LED at ca. 1800 μW/cm^2 attracted significantly more mated females than did one 350-nm LED at ca. 100 μW/cm^2.

Experiments 18 and 19: electroretinogram recordings

Eyes of males (experiment 17, n = 6) and females (experiment 18, n = 6) were exposed in alternating sequence to 350- and 405-nm wavelengths at a light intensity of 20 μW/cm^2 emitted from LEDs. Each LED was inserted into a reflective foil-covered 2-ml pipette tip (T-100-C; Axygen Scientific, Union City, CA, USA), with 2.3-cm clearance between the LED and the tip. The LED was calibrated to 20 μW/cm^2 using an HR4000 high-resolution spectrometer (Ocean Optics) fitted with a cosine corrector at the detector. For calibration, the pipette tip was positioned 1 mm apart from the detector, with the light spot focused at the middle of the detector surface, and intensities were measured using an integration of 300 to 450 nm. For electroretinogram recordings, the pipette tip was positioned 1 mm above the eye, delivering a 0.5-s flash of light controlled by a programmable timer. Between exposures, insects were dark-adapted for 20 min. Electrical potentials in response to light stimuli were normalized to the greatest response amplitude. Eyes of males (experiment 18) and females (experiment 19) responded significantly more strongly to the 405- than to the 350-nm LED (Figure 8).

Discussion

Our data support the conclusion that IMM uses violet light in addition to UV light as an orientation cue. Gender and mating status of IMM appear to affect their responsiveness to light. Our observations that males and mated but not virgin females engage in prolonged flights are well-reflected in the percentage of IMMs that are captured in light-emitting traps (Figures 3–6). Similarly, pheromone-emitting virgin females of the almond moth, *Ephestia cautella* (Walker), hardly take flight, whereas conspecific males engage in prolonged flights (Hagstrum & Davis, 1980). Captures of males and gravid females of the hemlock looper, *Lambdina fiscellaria* (Guenée), in UV light traps (Delisle et al., 1998) were attributed to searching behavior for mates and oviposition sites, respectively. In all our experiments (Figures 3–6), the percentage of gravid

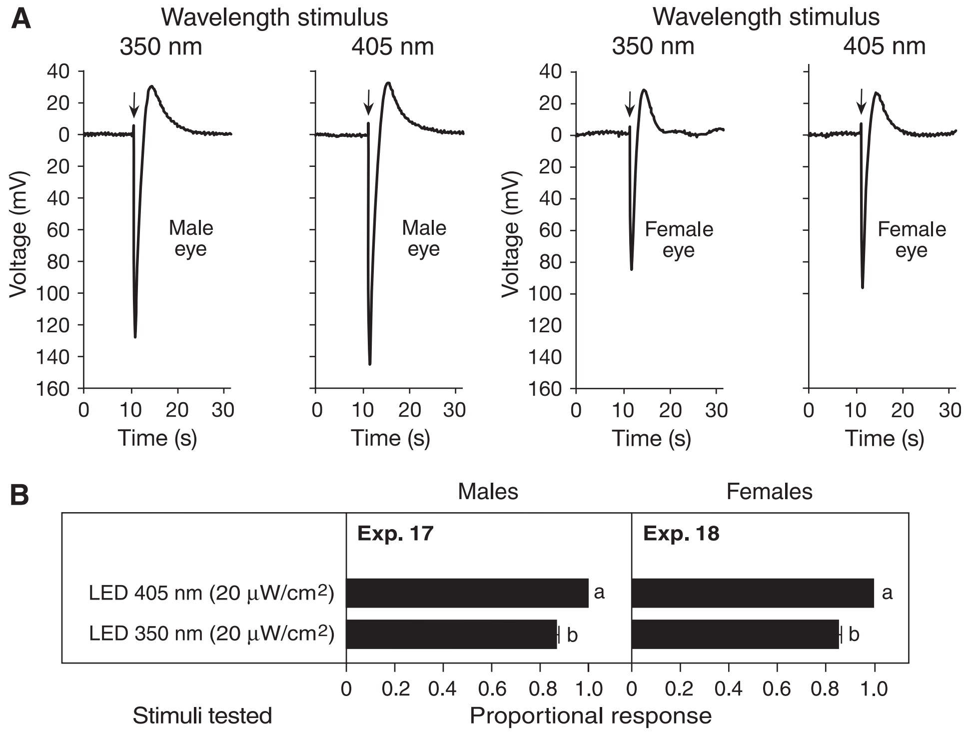

Figure 8 (A) Representative electroretinograms of eyes of male (left) and female (right) *Plodia interpunctella* responding to 405- and 350-nm wavelengths at 20 µW/cm^2 each; arrows indicate the onset of the 0.5-s light stimulus; (B) mean (+ SE) proportion of electrical potentials elicited by eyes of male and female *P. interpunctella* in response to 405- and 350-nm wavelengths. Bars with a different letter are significantly different (Wilcoxon rank sum test: $P<0.05$).

females responding to attractive light exceeded that of males or virgin females. These results contrast with those reported by Soderstrom (1970) that 2–3 times more males than females responded to traps emitting green or UV light. Based on our results and those cited above, it appears that mating induces a behavioral reversal from sedentary pheromone emission to dispersal or searching flight coupled with a strong phototactic response. Our conclusion that UV and violet light are orientation or navigation cues, rather than nectar guides in flowers, is supported by reports that IMM rarely feeds (Nansen et al., 2003; Olsson et al., 2005a,b).

Stronger orientation to blue than to green light by both males and gravid females (Figure 3) contrasts with previous conclusions (Stremer, 1959) that green is more attractive than blue light. These contrasting conclusions may be due, in part, to contrasting experiment designs. Stremer (1959) in no-choice experiments tested UV, green, or violet light (404.7 nm) as a single test stimulus at 9 µW/cm^2, whereas we tested in 2- or 4-choice experiments light stimuli at 15 µW/cm^2 each. In electroretinograms, green wavelengths elicited the strongest response but there was also suggestive evidence for a potential 'blue receptor' sensitive to wavelengths of ca. 460 nm (Marzke et al., 1973). If the spectral response pattern of photoreceptors were indicative of the wavelengths needed for orientation, then green light should have been the most effective orientation cue. Strong attraction to blue light instead (Figure 3) suggests that electroretinograms have limited value in predicting the wavelengths that play key roles during the insects' orientation behavior. They provide information, however, about the wavelength range an insect can see.

Known blue receptors in Lepidoptera exhibit peak sensitivity near 460 nm (Eguchi et al., 1982; Briscoe & Chittka, 2001). Strong attraction of male and female IMM to the 405-nm violet LED, and hardly any attraction to the 435-, 450-, and 470-nm blue LEDs (Figure 4), indicates that the violet region of visible blue light is used for orientation. This peak response to violet-blue light is likely not mediated by a blue-light receptor. For example, blue photoreceptors of the tobacco hornworm, *Manduca sexta* L., induce feeding responses and are most sensitive to a 'mid' 450-nm wavelength, with shorter or longer wavelengths eliciting weaker behavioral responses (Cutler et al., 1995). Indian meal moths do not show such responses towards blue light.

There are two possible explanations for the profound attractiveness of the 405-nm violet LED. First, IMM may detect violet light with the tail end of a UV receptor. This would explain why males, virgin, and mated females orient more strongly to the 350- than to the 405-nm violet LED (Figure 5). Second, the strong response to violet light (Figure 4) may be due, in part, to specific properties of the green photoreceptor. The main α-band and small β-band of green receptors absorb green and UV light, respectively (Stavenga, 2006). Conceivably, weak but concurrent stimulation by violet light of both the green receptors' β-band and specific UV receptors may trigger strong electrophysiological (Figure 8) and behavioral responses (Figure 4) to violet light.

Increasing the intensity of attractive wavelengths of light resulted in correspondingly stronger attraction of IMM (Stremer, 1959; Cowan & Gries, 2007, US and PCT patent applications). These results present intriguing prospects for manipulating the behavior of IMM in pest management settings, and inspired the design of experiment 15 (Figure 7). Considering that visible-light LEDs are capable of emitting higher light intensities, and are less expensive and less damaging to human eyes than UV LEDs, we offered gravid female moths a choice between two 350-nm LED and a combination of one 350- and one 405-nm LED with a greater combined light intensity. Stronger attraction of females to the LED combination (Figure 7, experiment 15), equal attraction to equal-intensity 405-nm lights with or without UV component (Figure 7, experiment 16), and stronger attraction to a 405- than to a 350-nm LED at maximum light intensities (Figure 7, experiment 16) all indicate that deployment of 405-nm LEDs should be considered as one of several possible tactics (Svensson et al., 2003) within integrated management programs for IMM.

Acknowledgements

We thank Inigo Novales Flamarique for valuable advice, Pilar Cepida for technical assistance in bioassays, Bob Birtch for graphical illustrations, Sharon Hope for word processing, Eberhard Kiehlmann for proofreading, and two anonymous reviewers for constructive comments. The research was financially supported by a Simon Fraser University Graduate Fellowship, a Professor Thelma Finlayson Graduate Entrance Scholarship, a Professor Thelma Finlayson Fellowship, and a Dr John Yorston Memorial Graduate Scholarship in Pest Management to Thomas Cowan, and by a Natural Sciences and Engineering Research Council of Canada – Industrial Research Chair to Gerhard Gries with Pherotech International, SC Johnson Canada, and Global Forest Science (GF-18-2007-226; GF-18-2007-227) as industrial sponsors.

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